may validate its defense throughout the year. Additional studies could test for this and other possible benefits for *D. pumilio* of territoriality during the non-reproductive season.

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Alternative mating strategies of *Megaloprepus coerulatus*

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Abstract: Territoriality can increase fitness by providing access to resources, shelter, and mates, but can also be energetically costly and may not be an option for all individuals if suitable potential territories are limited. Some male helicopter damselflies (*Megaloprepus coerulatus*) at La Selva Biological Station, Costa Rica, defend waterholes in forest light gaps against conspecific males; this is usually regarded as their only viable reproductive strategy. However, the population of adults seems larger than could be sustained by the number of light gap waterholes. This suggested the possibility of an alternative reproductive strategy for males without light gap waterholes. Artificial waterholes placed in gaps were occupied and defended by males within an hour of their placement. Furthermore, a female visited, mated, and oviposited in one of the artificial waterholes. Female mating and oviposition is only rarely observed about once per 84 days of observation; this suggests that waterholes are limiting for females as well as males. Although territoriality seems to be the preferred reproductive strategy for *M. coerulatus* , sneaking/understory reproduction may permit some reproduction for males that are unable to obtain a light gap waterhole. Furthermore, this alternative reproductive tactic may account for a meaningful proportion of the adult population of *M. coerulata* at La Selva.

Key Words: Gynacantha, helicopter damselfly, *Odonata Pseudostigmatidae*, sneakers, territoriality

Introduction

The reproductive success of males in territorial species is often limited by the availability of suitable territories. If territoriality is to be a viable mating system, and therefore an evolutionary stable strategy, the benefits of territoriality, such as better food resources and higher mating success, must outweigh the costs, such as investment in territorial defense and increased predation risk. The low density of suitable reproductive sites probably limits the population of *Megaloprepus coerulatus*, (helicopter damselflies) in the neotropical lowland wet forest of La Selva, Costa Rica.

Studies of Panamanian populations of *M. coerulatus* suggest that mating behavior is strongly structured around territorial males (Finke 2000), who defend semi-permanent water-filled treeholes in forest light gaps. The holes are usually at least 1.5 liters in volume, and are used for egg deposition and larval habitat. Defense of the hole by territorial males appears to occur before, during, and after copulation with a female. A second population of non-territorial or satellite males also mate, but it is not known how much reproduction by these males contributes to the population. Most eggs fertilized by these males are probably deposited in understory waterholes, which are thought to provide lower quality larval habitat, but sometimes they may also be surreptitiously deposited in waterholes within light gaps. Although this appears to be an inferior strategy, reproduction that involves satellite males may nonetheless be important for the population as a whole as it seems unlikely that the population of *M. coerlatus* at La Selva can be accounted for by the limited number of territorial males and light gap waterholes (Fred SaintOurs, pers. com.). This is especially true because of the long larval development time (95 d), and the intense intra and interspecific competition and predation within light gap waterholes.

Contrary to conventional understanding, it may be that both territoriality and the satellite tactics of males are viable reproductive strategies, working in tandem to maintain the *M. coerlatus* population at La Selva. If the sneaking technique is a successful reproductive strategy for male *M. coerlatus* at La Selva, then when given the opportunity to establish itself at an unclaimed light gap waterhole, a satellite male should not necessarily exhibit the costly, risky, defensive behavior common to territorial males. If territoriality were the only viable reproductive strategy, satellite males presented with an unclaimed light gap waterhole should rapidly adopt defense-related behaviors.

Methods

We observed *M. coerulatus* behavior in 4 forest gaps within 1 km of La Selva Biological Station, Costa Rica, from 0930 - 1500 for three days (15 - 17 February 2000). During observations, we recorded the time, duration, and location of all *M. coerulatus* activities (perch, forage, fly, and hover), taking special note of any interactions with *Mecistogaster liniarus* and *Mecistogaster modesta* (two other pseudostigmatid damselflies at La Selva), and of *Gynacantha* sp., a large forest-dwelling dragonfly. One male *M. coerulatus* from Gap I was captured and marked on day 1 to differentiate him from other males. On day 1, we observed Gaps I and II, which had no waterholes, and Gaps III and IV, which contained natural waterholes. At 0900 on day 2, artificial waterholes were placed in Gaps I and II, and left for the remainder of our observations. We investigated all the waterholes at the end of each day and determined whether or not larvae were present.

To test for (1) male behavioral differences among males and (2) behavioral differences before and after the addition of artificial waterholes, we classified the typical behavior of each male during each 30 minute interval throughout the observation period and applied chi-square contingency tests. Gap IV was excluded from these analyses because it lacked adequate observation time.

Results

All natural and artificial waterholes were defended by *M. coerulatus* males. The proportion of time that *M. coerulatus* spent in gaps was higher in gaps with natural waterholes than in gaps without waterholes (Table 1). Under the null hypothesis of no differences among individuals, males in Gaps I and II guarded less than expected and were absent from the gap more than expected on day 1, while the reverse was true for the male in Gap III (Table 2; $X^2 = 28.19$, df = 6, $p < 0.001$). There was no difference in behavior among individuals on days 2 and 3 ($X^2 = 7.22$, df = 6, p = 0.301). In Gap I, the marked male was present for 137 min on day 1, but did not return after day 1. Gap II was visited for a total of 1 min on day 1 by a single male.

The behavior of individuals in experimental gaps was affected by the addition of artificial waterholes. Males in these gaps guarded territories less than expected and were absent from the gap more than expected before the addition of the waterhole. Post-treatment, males guarded territories more than expected, and were absent from gaps less than expected (Table 3; $X^2 = 25.18$, df = 6, p = 0.002). On day 2 a male occupied Gap I within 30 min of the placement of the artificial waterhole. This new individual defended the gap for the next two days, engaging in and dominating conspecific aggressive interactions on both days. This male engaged in copulation on day 3 and the female deposited eggs in the artificial hole. In Gap II a male also arrived within 30 minutes and began defending the artificial waterhole on day 2. This male remained throughout days 2 and 3. This male spent 57-88% of the observation time during days 2 and 3, respectively, perching 2

Table 1. Time budgets for *M. coerulatus* individuals in gaps within 1 km of La Selva Biological Station, Costa Rica, as proportion of time spent in given activity over each day. Observations were continuous from 9:30 - 15:00 on 15 - 17 February, 2000.

	Gap I day			Gap II day			Gap III day			Gap IV day		
Status	1	2	3	1	2	3	1	2	3	1	2	3
perching	0.70	0.82	0.28	0.00	0.57	0.88	0.77	0.57	0.61	0.63	0.22	0.43
foraging	0.03	0.03	0.00	0.01	0.01	0.01	0.04	0.06	0.05	0.09	0.58	0.25
flying	0.04	0.06	0.00	0.00	0.02	0.02	0.04	0.03	0.01	0.00	0.00	0.11
hover	0.00	0.02	0.03	0.00	0.00	0.00	0.02	0.02	0.01	0.00	0.01	0.00
interaction	0.00	0.01	0.07	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00
out of sight	0.13	0.06	0.53	0.99	0.37	0.09	0.02	0.24	0.27	0.27	0.19	0.21
other[a]	0.10	0.00	0.09	0.00	0.00	0.00	0.12	0.07	0.05	0.00	0.00	0.00

[a] Includes interactions with non-conspecifics, searching for hole in pre-treatment site, and dipping in the hole. Proportion on day 3 in Gap I represents time spent in mating behavior, including courting and copulation.

m or less from the artificial hole.

Gap III was occupied by one male on all three days. He spent 77%, 57% and 61% of the time observed on days 1, 2 and 3, perching 1.5 m or less from the natural water hole in that gap. Gap IV was also occupied by one male on all three days whose behavior was consistent across days 1, 2, and 3. In general, he seemed to perch and forage farther from the waterhole (up to 40 m away) than the Gap III male.

G. gracilis dragonflies, which also require waterholes for breeding, visited all gaps. *G. gracilis* ovipositions were observed in the waterholes of Gaps I and IV while *M. coerulatus* males were perched within 1 meter of the waterholes. There was no apparent interaction between the *G. gracilis* and *M. coerulatus* adults. One *G. gracilis* larva (3.0 cm long) was found in the Gap IV waterhole, and mosquito larvae were present in the Gap III waterhole.

Discussion

Our results suggest that territoriality is the preferred mating strategy of male *M. coerulatus* at La Selva. The almost immediate defense of artificial waterholes in gaps where territorial behavior had not previously been observed suggests that males are constantly and actively seeking a suitable territory, and will readily adopt a territorial strategy whenever these waterholes become available. Apparently, male reproductive success is limited by the availability of light gap waterholes. In addition, the speed with which a female presented herself at the artificial waterhole (within 2 d), and the subsequent copulation

Table 2. Behavior of *M. coerulatus* males. Data are number of 30 min observation periods on day 1, characterized by different possible behavior classes in three different light gaps.

Behavior	Gap 1	Gap 2	Gap 3
Flying/Foraging	2	0	1
Guarding hole[a]	1	0	7
Perching	3	0	0
Unseen	12	9	1
Sum	18	9	9

[a] Guarding included interactions with conspecifics, hovering above the hole, and perching ≤ 2 m over the hole.

Table 3. Behavior of *M. coerulatus* males before and after the placement of artificial waterholes. Data are number of 30 min observation periods, characterized by different possible behavior classes on day 1 (pre-treatment), and days 2 and 3 (post-treatment).

Behavior	Day 1	Day 2	Day 3
Flying/Foraging	2	0	3
Guarding hole[a]	1	10	12
Perching	3	3	3
Unseen	21	7	6
Sum	27	20	22

[a] Same as Table 2.

and oviposition events, argues that males defending light gap waterholes have generally higher fitness as compared to satellite males.

The rapidity with which females located and oviposited in the artificial waterholes indicates that females also are seeking new potential breeding ground. Fred SaintOurs (pers. com.) indicated that he had previously observed only two copulations during 24 weeks of field study. Male behavior may intensify waterhole limitation among females, as a male often will try to prevent females with whom he has not mated from ovipositing at his waterhole (Finke 2000). Intraspecific interactions are also likely to influence the reproductive success of both sexes in waterholes. *G. gracilis* larvae occupy the same type of waterholes as *M. coerulatus* and prey upon *M. coerulatus* whenever the two species co-occur (Finke 2000). This intense competition, however, seems to be limited to the larval stages. In the two cases where *G. gracilis* were observed ovipositing at the natural waterholes, the male *M. coerulatus* did not move from his perch to challenge the *G. gracilis*, even though he actively defended his hole against conspecifics throughout the day.

The paradox of the persistence of the La Selva *M. coerulatus* population remains. If males without territories must wait until a suitable territory becomes available before reproducing, it is difficult to reconcile the apparently low number of suitable waterholes with a population estimated to include at least 20 individuals that were visiting or occupying two light gaps. Of course, there must be more light gap waterholes at La Selva than we found, but this cannot account for the population of adults in the light gaps we studied unless the proportion of light gaps that contain suitable waterholes is much higher in the light gaps we did not search. It seems more likely that sneaking/understory reproduction accounts for a larger proportion of the *M. coerulatus* population than suspected. This suggests that *M. coerulatus* employs a mixed reproductive strategy in which territoriality is preferred, but the sneaking/understory tactics also allow some reproductive success. More extensive searches for light gap waterholes and further exploration of understory waterholes for *M. coerulatus* larvae would provide information about the relative contributions of alternative reproductive strategies to *M. coerulatus* at La Selva.

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